

It takes a few to tango: Interactions between changing climate and fire regimes can cause regeneration failure of two subalpine conifers

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19 *Abstract.*

20 Environmental change is accelerating in the 21st century, but how multiple drivers may interact
21 to alter forest resilience remains uncertain. In forests affected by large high-severity
22 disturbances, tree regeneration is a resilience linchpin that shapes successional trajectories for
23 decades. We modeled stands of two widespread western US conifers, Douglas-fir (*Pseudotsuga*
24 *menziesii* var. *glauca*) and lodgepole pine (*Pinus contorta* var. *latifolia*), in Yellowstone National
25 Park (Wyoming, USA) to ask: (1) What combinations of distance to seed source, fire return
26 interval and warming-drying conditions cause postfire tree-regeneration failure? (2) If postfire
27 tree regeneration was successful, how does early tree density differ under future climate relative
28 to historical climate? We conducted a stand-level (1 ha) factorial simulation experiment using
29 the individual-based forest process model iLand to identify combinations of fire return interval
30 (11 to 100 years), distance to seed source (50 to 1000 m), and climate (historical, mid-21st
31 century, late-21st century) where trees failed to regenerate by 30-years postfire. If regeneration
32 was successful, we compared stand densities between climate periods. Simulated postfire
33 regeneration were surprisingly resilient to changing climate and fire drivers. Douglas-fir
34 regeneration failed more frequently (55%) than lodgepole pine (28% and 16% for non-serotinous
35 and serotinous stands, respectively). Distance to seed source was an important driver of
36 regeneration failure for Douglas-fir and non-serotinous lodgepole pine; regeneration never failed
37 when stands were 50 m from a seed source and nearly always failed when stands were 1 km
38 away. Regeneration of serotinous lodgepole pine only failed when fire return intervals were ≤ 20
39 years and stands were far (1 km) from a seed source. Warming climate increased regeneration
40 success for Douglas-fir but did not affect lodgepole pine. If regeneration was successful, postfire
41 density varied with climate. Douglas-fir and serotinous lodgepole pine regeneration density both

increased under 21st-century climate but in response to different climate variables (growing season length vs cold limitation). Results suggest that given a warmer future with larger and more frequent fires, a greater number of stands that fail to regenerate after fires combined with increasing density in stands where regeneration is successful could produce a more coarse-grained forest landscape.

Keywords: *Climate change; Drought; Forest resilience; Process-based modeling; Seedling establishment; Wildfire; Succession; Yellowstone National Park*

INTRODUCTION

Forests will experience increased stress as environmental change accelerates in the 21st century (Millar and Stephenson 2015, Trumbore et al. 2015). It remains poorly resolved whether forests will prove resilient and recover from these perturbations (Scheffer 2009) or instead transition to alternate states (Ghazoul et al. 2015, Reyer et al. 2015). Resilience is defined as the capacity of a system to absorb disturbances while retaining function, structure, feedbacks, and thus, identity (Walker et al. 2006). It is plausible that whole forested regions, such as the Amazon and boreal forest, may prove vulnerable to environmental change (Lenton et al. 2008, Hirota et al. 2011, Scheffer et al. 2012, Gauthier et al. 2015). Yet, quantifying forest resilience is challenging because multiple drivers, like natural disturbances, drought, land use, and nitrogen deposition will act on forests simultaneously, causing compound effects that are difficult to anticipate (Paine et al. 1998, Savage and Mast 2005, Staal et al. 2014, Buma 2015, Littell et al. 2016). Further, heterogeneity in abiotic conditions (e.g., substrate, elevation, aspect) and variation in tree functional traits (among and within species) can amplify or dampen driver effects (Lamont and Enright 2000, Chmura et al. 2011, Hoffmann et al. 2012, Johnstone et al. 2016). Thus,

studies identifying interactions among multiple drivers that influence forest resilience could yield substantial insight into how and why 21st-century forests may change.

Regional forest change will likely emerge from the effects of environmental drivers on local- and landscape-scale processes (e.g., dispersal, seedling establishment, tree growth, competition, and mortality) (Peters et al. 2004, 2007, Turner 2010). In forests where large wildfires kill most trees (i.e., stand-replacing fire), tree regeneration is a resilience linchpin (Turner et al. 1998, Johnstone and Chapin 2006, Johnstone et al. 2010, Savage et al. 2013) because seedling establishment in the first few years after disturbance dictates species composition and stand structure for decades to centuries (Kashian et al. 2005, Martínez-Vilalta and Lloret 2016). Robust postfire tree regeneration requires sufficient seed supply and delivery. Fire activity is projected to increase globally (Pechony and Shindell 2010, Seidl et al. 2014, 2017, Abatzoglou and Williams 2016) and postfire seedling densities may be reduced if burned patch sizes exceed effective dispersal distances or if multiple fires reoccur before trees reach reproductive maturity (Keeley et al. 1999, Enright et al. 2014, 2015, Kemp et al. 2016, Harvey et al. 2016a, Johnstone et al. 2016, Stevens-Rumann and Morgan 2016, Chambers et al. 2016). When seed is available, changing climate can also shape regeneration outcomes because tree seedlings are very sensitive to environmental conditions (Walck et al. 2011). Warming could reduce establishment if severe droughts follow fires (Clark et al. 2016, Harvey et al. 2016a) or warming could enhance establishment by reducing frost damage (Inouye 2000) and lengthening the growing season.

It is challenging to disentangle the effects of multiple drivers on postfire regeneration, but process-based models offer a promising approach when empirical studies cannot capture the full range of potential conditions. Large, short-interval fires and severe postfire droughts may

become more prevalent in the western US (Westerling 2016) but still occur infrequently in subalpine forests. Thus, opportunities to observe in the field how combinations of changing fire and drought affect tree regeneration across heterogeneous landscapes are scant. Further, the magnitude of projected 21st-century environmental changes, their complex interactions, and the potential for emergent feedbacks suggest that future ecosystem dynamics may be difficult to predict solely based on current observation (Gustafson 2013, Bowman et al. 2015). However, process-based models allow exploration of a more complete set of conditions than found in the field and should provide robust projections under novel conditions because they are based on ecological first principles rather than empirical relationships (Seidl et al. 2011, Keane et al. 2015, Gustafson 2013). Models also can help distill complex phenomena down to essential components and highlight gaps in ecological understanding (Grimm and Berger 2016, Dietze 2017, Seidl 2017).

Yellowstone National Park (Wyoming, USA) is an excellent place to study how changing climate and fire regimes may alter postfire tree regeneration. Subalpine forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) experienced large stand-replacing fires at 100 to 300 year intervals during the Holocene (Millspaugh et al. 2000, Power et al. 2011). Postfire tree regeneration has generally been robust following fires (Turner et al. 1997, 2004, 2016). Some lodgepole pine trees in Yellowstone develop serotinous cones that remain closed and accumulate for many years; when heated by fire, they open and drop large quantities of seed. Other lodgepole pines produce only non-serotinous cones that open as they mature. (Tinker et al. 1994). Lower montane forests are dominated by more drought tolerant Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Warming and increased drought during the 21st century are projected to cause marked increases in the size, severity, and frequency of wildfires (Westerling et al. 2011)

and alter the environmental context in which trees reestablish. The magnitude of expected change may be inconsistent with current forest structure and tree-species composition, meaning that forests could change profoundly (Hansen and Phillips 2015, Clark et al. 2017).

We conducted a factorial simulation experiment to evaluate effects of changing fire regimes and postfire climate conditions in Yellowstone on regeneration of two widespread Rocky-mountain conifer tree species, lodgepole pine and Douglas-fir. We asked two questions. (1) *What combinations of distance to seed source, fire return interval (FRI) and warming-drying conditions cause postfire tree-regeneration failure?* We hypothesized that postfire regeneration failure would be more likely if seed delivery was reduced by increasing distance to seed source (i.e., a proxy of increasing fire size or changing perimeter shape), if seed supply decreased with shortened FRI because trees burned before reaching maturity, or if postfire drought reduced seedling establishment (Table 1). We also expected that lodgepole pine and Douglas-fir would differ in their responses. We hypothesized Douglas-fir regeneration would be most sensitive to distance to seed source because Douglas-fir produce fewer relatively heavy seeds and rely on adjacent unburned forests for seed delivery; non-serotinous lodgepole pine regeneration would show intermediate sensitivity because they produce a greater number of lighter seeds; and serotinous lodgepole pine regeneration would be least sensitive due to the canopy seedbank. However, we expected serotinous lodgepole pine to be very sensitive to shortened FRIs that burn stands before the canopy seedbank develops. (2) *If postfire tree regeneration was successful, how does early postfire tree density differ under future climate relative to historical climate?* We hypothesized that, once trees established, their postfire densities would be sensitive to variation in climate such that increasing drought frequency and severity would be associated with reduced tree density. We also expected that early postfire Douglas-fir densities would be less affected by

future drought than lodgepole pine because Douglas-fir are physiologically adapted to drier conditions.

STUDY AREA AND METHODS

Study area

Yellowstone National Park encompasses approximately 9,000 km² in northwestern Wyoming, USA. Elevation ranges from 1,600 m to 3,400 m, with lower tree line at 1,800 m and upper tree line at 3,050 m (Despain 1990). Climate is relatively warm and dry in the lower montane zone where Douglas-fir is common, with a mean July temperature of 17.5°C and 390 mm of annual precipitation (Western Regional Climate Center 2017). Climate is cooler and wetter in the higher-elevation subalpine zone, with a mean July temperature of 14°C and annual precipitation of 584 mm. Forest soils are generally derived from volcanic parent material, typically rhyolite or andesite. Rhyolite-derived soils have less mineral nitrogen (Whitlock 1993) and poor water holding capacity (Simard et al. 2012) compared to soils derived from andesite (Despain 1990), but both are considered infertile. Douglas-fir and lodgepole pine are obligate seeders, and in Yellowstone, both experience stand-replacing fire. Seeds are wind dispersed, and most seeds fall within 100 m of the source (Burns and Honkala 1990). Following the iconic 1988 Yellowstone fires, which burned two-thirds of the park, Douglas-fir and lodgepole pine both reestablished successfully, albeit with substantial variability across the landscape. Early (24 year) post-1988 fire Douglas-fir stand densities ranged from 0 to 19,667 stems ha⁻¹ with a median of 1,250 stems ha⁻¹ (Donato et al. 2016); postfire (24 year) lodgepole pine densities ranged widely, from 0 to >340,000 stems ha⁻¹ with a median density of 4,050 stems ha⁻¹ (Turner et al. 2016). Stands where prefire serotiny was high account for the denser postfire regeneration. Stands

where prefire serotiny was low had postfire densities ranging from 600 to 2,300 stems ha⁻¹ (Turner et al. 1997, 2004).

Model overview and simulation experiment

We simulated stand-level (1-ha) dynamics using an individual-based forest process model, iLand (Seidl et al. 2012, 2014). iLand simulates trees within a stand and uses a hierarchical framework wherein broader-scale processes emerge dynamically from interactions among individual trees (Seidl et al. 2012). iLand represents tree growth, mortality, and competition in response to canopy light interception, radiation, thermal conditions, soil water, and nutrient limitation. While climate and soil conditions are assumed to be spatially homogeneous within a stand (1 ha), variation in light is simulated at 2×2m horizontal resolution based on overstory structure and composition. Climate variability is considered at a daily temporal grain. iLand also simulates disturbances. Extensive model documentation is available online (<http://iland.boku.ac.at>). The model has been well tested and extensively used in the western United States (Seidl et al. 2012, 2014) and Europe (Pedro et al. 2015, Thom et al. 2017a, 2017b), and has recently been parameterized and evaluated for Yellowstone (a full parameter set is available online: www.github.com/whansen3/Hansen_stand_level_archive).

The model explicitly simulates tree regeneration based on seed production, seed dispersal, and effects of temperature, light, and soil-moisture conditions on seedling establishment and survival (Seidl et al. 2012) (Appendix S1). We extended the regeneration module of iLand in two ways. First, we added serotiny as a functional trait for lodgepole pine. Serotinous lodgepole pine only drop seeds in the year following a fire. When trees are serotinous, the amount of seed released is a multiple of the seeds produced by a non-serotinous tree, representing the accumulation of cones over multiple years. We further incorporated an

effect of soil moisture on rates of seedling establishment in addition to the already existing temperature limitation. The probability of seedling establishment at a 2m cell is linearly scaled between a species-specific minimum soil water potential, where establishment does not occur, and field capacity, where establishment is not constrained by soil moisture. We evaluated the improved regeneration module of iLand and simulated tree establishment agreed well with independent field observations (Appendix S2).

Initial stand structure. Simulations were initialized with a representative monospecific stand for each forest type using median stem density and tree heights for each forest type as recorded 11 years after the 1988 Yellowstone fires (Turner et al. 1999, 2004, 2016, Donato et al. 2016). We chose not to vary initial stand structure within each forest type because we were interested in experimentally testing climate-fire interactions and therefore we minimized other sources of variation.

Topoedaphic conditions. Our simulations did include variation in substrate and elevation, because both influence tree establishment, and thus, are important for addressing our questions. We simulated soils derived from two volcanic parent materials, rhyolite and andesite, which account for most of Yellowstone's subalpine landscape (Despain 1990). Relative fertility rating (calibrated within iLand to 45 and 55 for rhyolite and andesite, respectively, on a [0-100] scale) and soil texture (62% sand, 30% silt, 8% clay for rhyolite, 51% sand, 37% silt, 12% clay for andesite) were set according to representative soil surveys conducted throughout Yellowstone (Turner et al. 1999, Simard et al. 2012). For all soils, effective depth was set to 95 cm. Elevation was included by simulating stands at lower treeline (2,000 m), as well as the mid (2,300 m), and high elevation (2,600 m) of the subalpine zone. These span the elevational range in which Douglas-fir and lodgepole pine are found regionally.

Factorial simulation experiment. We conducted a factorial experiment using iLand to evaluate how combinations of climate and fire conditions affected early (30 year) postfire tree regeneration of Douglas-fir, non-serotinous lodgepole pine, and serotinous lodgepole pine. Thirty years was selected as a benchmark for assessing regeneration because it accommodates the more protracted establishment window of conifers that lack a canopy seedbank (Turner et al. 1999, Donato et al. 2016), captures longer-term effects of climate on young trees, and largely avoids the self-thinning that occurs in dense stands during later periods of stand development. The factors considered in the experiment for all forest types were FRI, distance to seed source, and variation in climate and they were applied to every combination of the two substrates and three elevations.

Return interval for high-severity fire. Effects of FRI were simulated by burning stands at age 11, 20, 50, or 100 yrs. Simulated FRI spanned the range from short-interval fires projected by the end of the 21st century (Westerling et al. 2011) and observed in Yellowstone (e.g., the 2000 Boundary Fire burned 12-yr old lodgepole pine that regenerated from the 1988 fires) to the lower end of FRIs observed during the Holocene (Millsbaugh et al. 2000). Stand development was simulated until the specified FRI was reached, at which time stand-replacing fire killed all prefire trees, saplings, and seedlings.

Distance to seed source. We simulated stands at distances of 50 m, 500 m and 1 km from the nearest unburned seed source which could either represent forest at the fire edge or islands of unburned forest in the middle of burned patches. In actual fires, distance to seed source is primarily a function of the size and shape of high-severity burned patches. Seed supply and dispersal were modeled with species-specific negative exponential dispersal kernels and compared with field surveys (Appendix S1, S2).

Variation in climate. Effects of climate were simulated by driving the model with climate from three 30-year periods. We used a historical period (1950 to 1980) and two levels of climate change that represented a temperature increase of 3 and 5.5 °C, indicative of mid-century (2029-2059) and late-century (2069-2099) warming under the Representative Concentration Pathway (RCP) 8.5. The RCP 8.5 scenario represents a substantial increase in CO₂ over the next 100 years, although current trends suggest this emissions scenario is already being exceeded (Smith et al. 2016). We used the CNRM-CM5 global circulation model (GCM) (Voldoire et al. 2013), which reproduces historical conditions in the northern Rockies well (Westerling et al. 2011). Climate variables that drive iLand simulations include maximum and minimum daily temperature, daily precipitation, radiation, and vapor pressure deficit. Climate data were statistically downscaled to a 4-km resolution using the Multivariate Adaptive Constructed Analogs approach (Abatzoglou and Brown 2012) (URL: <http://maca.northwestknowledge.net/index.php>). Data were extracted for one grid cell per elevation that corresponded to a median density field plot. We chose only one grid cell per elevation because we were not attempting to characterize effects of climate variation within elevation bands, but rather across the elevational range of the species' current distributions.

Replication. Simulations were each run 20 times and years were drawn randomly with replacement from the appropriate 30-year climate record to ensure the order of the climate record did not influence simulation results. This led to 20 replicates of each forest type (3 levels), substrate (2 levels), elevation (3 levels), FRI (4 levels), distance to seed source (3 levels) and climate (3 levels) combination.

Model outputs

We focused on two model outputs: frequency of regeneration failure at 30 years postfire (Question 1) and, if regeneration was successful during the historical climate period, the difference in mean tree density between historical and projected 21st-century climate (Question 2). Regeneration failure was defined as stands that had < 50 stems ha⁻¹ (including seedlings, saplings, and young trees) at postfire-year 30, which would indicate potential transition to a non-forest condition. The United Nations Food and Agricultural Organization (FAO) defines forest as any area > 0.5 ha that has $> 10\%$ canopy cover (Chazdon et al. 2016). Our threshold of 50 stems ha⁻¹ in Yellowstone would fall well below the FAO definition, and such densities are considerably lower than those commonly observed following recent fires in Yellowstone. For example, only 1.4% of early postfire (24 year) stands had densities < 50 stems ha⁻¹ after the 1988 Yellowstone fires (Turner et al. 2016). We then calculated the frequency of regeneration failure across the 20 replicates of each simulation. If regeneration was successful (i.e., ≥ 50 trees ha⁻¹) during the historical climate period, we calculated the difference in mean 30-yr postfire stem density between the historical and each projected 21st-century climate period.

Data analysis

To address Question 1 (regeneration frequency), we first used ANOVA to explain factors influencing the frequency of regeneration failure based on the levels of each treatment in the simulation experiment. We conducted analyses separately by forest type. We then explored the influences of climate in more detail, applying linear mixed-effects models (LMMs). We included mean growing-season temperature, mean annual precipitation, mean growing season soil water potential, and number of growing season frost events as fixed-effects. Random effects included non-climate related treatment-level variables (i.e., distance to seed source and fire return interval). This approach allowed us to ask, controlling for non-climate related factors, what

specific climate variables explained variation in response variables? We used the lme4 package in R (Bates et al. 2015) and all explanatory variables were assessed for collinearity. Variables were not included in the same model if they had a pairwise correlation of greater than 0.7. The dependent variable was transformed using a logit transformation. In regressions, all continuous variables were standardized prior to analysis. Exhaustive model selection (Burnham and Anderson 2002) was conducted in all analyses (ANOVA and LMM) to determine the most important variables using the R package MuMIn (Barton, 2015). Top models ($AIC_c < 2$) are presented for ANOVA and model-averages are presented for LMMs. Analyses were conducted in R statistical software (R Core Team 2016).

To address Question 2 (density differences), we first used ANOVA to explain differences in stand densities between the 21st century and historical periods, when regeneration was successful, for each forest type. We then used LMMs to identify climate variables that explained treatment level effects (as described above). A $\sqrt[9]{}$ transformation was applied to the dependent variable for serotinous lodgepole pine so that residuals were approximately normally distributed. All statistical analyses were conducted to efficiently find patterns in the simulated data as opposed to determine statistical significance. Thus, in results the magnitudes of difference between treatments are emphasized. In the text, means \pm one stand error are presented.

RESULTS

Across all simulations, Douglas-fir densities at postfire year 30 ranged from 0 to 21,186 stems ha⁻¹ (mean = $2,677 \pm 327$ stems ha⁻¹, median = 132 stems ha⁻¹). Non-serotinous lodgepole pine densities ranged from 3 to 3,197 stems ha⁻¹ (mean = 815 ± 62 stems ha⁻¹, median = 412 stems ha⁻¹). Serotinous lodgepole pine densities were between 7 and 93,972 stems ha⁻¹ (mean = $23,120 \pm 1,730$ stems ha⁻¹, median = 4,569 stems ha⁻¹). Simulated stand densities of these forest

types closely matched field observations of postfire densities in Yellowstone (Donato et al. 2016, Turner et al. 2016) (Appendix S2). In general, simulated densities decreased with distance to seed source and increased or stayed the same under 21st century climate, compared with historical conditions.

Frequency of regeneration failure (Question 1)

Douglas-fir. Douglas-fir failed to regenerate by postfire-year 30 in 55% of the simulations (Fig. 1), primarily due to distance from seed source (Table 2A, Fig. 2A). Regeneration was always successful if stands were 50 m from a seed source and nearly always failed when stands were 1 km away (Fig. 3A). Climate period was also an important driver, with regeneration failure declining from $64 \pm 6\%$ under historical climate to $41 \pm 5\%$ under late-21st century climate. When direct measures of climate were substituted for categorical variables, LMMs revealed that reduced failure of Douglas-fir regeneration in 21st-century climate periods was driven by fewer growing season frost events (Table 3A).

Non-serotinous lodgepole pine. Non-serotinous lodgepole-pine failed to regenerate by postfire-year 30 in 28% of simulations (Fig. 1). Like Douglas-fir, regeneration failure was most strongly determined by distance to seed source (Table 2A, Fig. 2B); failure was likely when stands were 1 km from a seed source and minimal when stands were 50 or 500 m away (Fig. 3B). Elevation and substrate had small effects on regeneration failure. Regeneration failure occurred more frequently at low (32%) versus high elevations (23%) and on rhyolite (29%) versus andesite substrate (26%). Climate period did not affect regeneration failure. LMMs revealed that the small effects of elevation and substrate reflected tradeoffs between drying soils, which increased regeneration failure, and reduced growing season frost events, which decreased regeneration failure (Table 3A).

Serotinous lodgepole pine. Serotinous lodgepole pine failed to regenerate by postfire-year 30 in < 20% of simulations (Fig. 1). Regeneration failure was driven by distance to seed source, FRI, and their interaction (Table 2A, Fig. 2C). Regeneration failure was more frequent when stands were 1 km from seed source and FRIs were ≤ 20 years (Fig. 3C). As with non-serotinous lodgepole pine, elevation had a small effect on regeneration failure (19% at low versus 13% at high elevation), and climate period was unimportant (Table 3B).

Density differences (Question 2)

Douglas-fir. Where regeneration was successful under historical climate, simulated regeneration density in postfire-year 30 averaged $1,205 \pm 114$ stems ha^{-1} . Postfire regeneration density increased nearly four fold (to $4,036 \pm 411$ stems ha^{-1}) under mid 21st-century conditions and six fold (to $7,893 \pm 776$ stems ha^{-1}) under late 21st-century conditions (Table 2B). Tree density increased only when stands were near (50 m) a seed source (Table 2B). Substrate also had a minor effect on density differences (Table 2B). LMMs revealed that stand densities increased with warming temperature and more precipitation (Table 3B, Fig. 4).

Non-serotinous lodgepole pine. Simulated stand densities averaged 800 ± 105 stems ha^{-1} in stands where regeneration was successful under historical conditions and changed little in mid (910 \pm 116 stems ha^{-1}) and late (790 \pm 71 stems ha^{-1}) 21st-century periods (Table 2B). Densities were also slightly greater at low elevations close to seed source (increasing to 971 \pm 32 stems ha^{-1}) (Table 2B) but did not change at mid or high elevations. LMMs suggest decreases in annual precipitation and drying soils explained variability in stand density differences (Table 3B).

Serotinous lodgepole pine. When regeneration was successful, simulated densities of serotinous lodgepole pine at postfire year 30 averaged $19,800 \pm 1,929$ stems ha^{-1} under historical conditions. Serotinous lodgepole pine densities increased by nearly 63% (by $12,505 \pm 2,123$

stems ha^{-1} to reach $> 32,000$ stems ha^{-1}) at low elevations during 21st-century periods (Table 2B). Stand densities increased with a FRI of 50 years (to $31,247 \pm 1,298$ stems ha^{-1}) or 100 years (to $26,013 \pm 1,566$ stems ha^{-1}) (Table 2B). Distance to seed source had a modest effect as well, with densities increasing to $27,900 \pm 1,927$ stems ha^{-1} at distances within 500 m of a seed source (Table 2B). Treatment level effects were explained by decreasing annual precipitation in the LMMs (Table 3B).

DISCUSSION

Results of this study indicate that regeneration of two conifers following stand-replacing fire in subalpine forests is shaped by the complex interplay among several drivers related to future climate and fire regimes, some that constrain regeneration and others that enhance it. Overall, postfire regeneration of Douglass-fir and lodgepole pine was surprisingly resilient to the substantial changes in climate and fire regimes projected for Yellowstone, particularly when drivers were considered individually. Simulated regeneration failure generally required multiple changing drivers (Fig. 2). Stand-level simulation experiments cannot predict how and where forests will change across the landscape, and results could differ in mixed-species stands. However, this study reveals complex responses to multiple changing drivers and offers insights into the mechanisms underpinning forest resilience (Trumbore et al. 2015, Reyer et al. 2015).

What causes regeneration failure (or success?)

Distance to seed source explained nearly all variation in regeneration failure for Douglas-fir and non-serotinous lodgepole pine, consistent with our hypotheses (Table 1). This finding suggests there are large consequences associated with projections of increased area burned during the 21st century (Westerling et al. 2011), as the size and shape of high-severity burn patches strongly determines regeneration of conifers that lack a canopy seed bank. Indeed, most

regeneration following recent fires in the northern Rocky Mountains has occurred within 150 m of the unburned edge (Kemp et al. 2016, Donato et al. 2016, Harvey et al. 2016a). Our findings are consistent with prior studies that emphasize the importance of biotic residuals (i.e., propagules or surviving trees within large disturbed patches) for regeneration following large, infrequent disturbances (Turner et al. 1994, 1998, Franklin and Forman et al. 1987, Franklin et al. 2002, Seidl et al. 2014, Johnstone et al. 2016, Tepley et al. 2017).

Regeneration failure was uncommon in serotinous lodgepole pine stands, which develop canopy seedbanks. Regeneration failure only occurred in stands far from seed source when fires burned again before the development of the canopy seed source (Fig. 2). Serotiny is an effective fire adaptation expressed in a variety of species globally (Lamont et al. 1991, He et al. 2012). Dense seed rain from cones that open after fire enables serotinous tree species to establish rapidly in postfire environments where a flush of resources is available and competition is low (Tinker et al. 1994, Keeley et al. 2005, Causley et al. 2016). Serotiny may also buffer against other drivers of postfire regeneration failure, including poor substrates for establishment (Johnstone and Chapin 2006, Johnstone et al. 2009), seed predation (Lamont et al. 1991; though see Benkman and Siepielski 2004), and postfire drought (Lamont and He 2017). This prolific production of seed may partly explain the lack of sensitivity to climate conditions in our simulation study. After the 1988 Yellowstone fires, postfire regeneration density in stands where prefire serotiny was high commonly exceeded 100,000 stems ha^{-1} . Even if hostile conditions reduce stand density by 90% a robust forest will grow back. Serotiny can be an effective bet hedging strategy for species facing variable environments (Buma et al. 2013).

Serotinous stands lose their advantage if fires reoccur before trees are reproductively mature (Buma et al. 2013, Johnstone and Chapin 2006). Thus, postfire densities of serotinous

species could be substantially reduced by short-interval fires, consistent with other systems where fire intervals are shortening (Keeley et al. 1999, Enright et al. 2015, Bowman et al. 2016). For example, serotinous black spruce (*Picea mariana*) seed supply was reduced 90% after short-interval fires in the Yukon Territories, Canada (Brown and Johnstone 2012). However, short FRIs alone were insufficient to initiate regeneration failure of simulated serotinous lodgepole pine stands in Yellowstone; burned stands also had to be far from seed source, limiting the seed supply from neighboring unburned stands.

Climate effects on regeneration failure differed by forest type. Warming enhanced Douglas-fir regeneration because frost events became less frequent during the growing season. Although growing season frost became rare in simulations under 21st-century conditions, warming could expose seedlings to winter frost damage if snow cover is reduced because snow insulates seedlings from temperature fluctuations (Batllori et al. 2009, Renard et al. 2016). Reductions in winter snowpack are projected to be greatest at mid elevations in Yellowstone versus high elevations, where snowpack is projected to remain consistent (Tercek and Rodman 2016), or low elevations, where snow pack is already less. Winter warming could also delay sapling spring growth initiation if chilling requirements are no longer met (Ford et al. 2016). The insulating effect of snow and winter chilling is not currently represented in iLand, and further study is needed to determine how winter climate change may counter effects of declining growing season frost.

Our study suggests substantial resilience of lodgepole pine stands to projected warming; non-forest states rarely occurred in the simulation with the combinations of factors considered here, although tree density could change substantially in the future (e.g., Schoennagel et al. 2006). In part, this may reflect our conservative definition of regeneration failure (< 50 stems ha⁻¹

¹ at postfire year 30) relative to the prolific regeneration capacity of lodgepole pine and its ability to produce cones at a young age (Turner et al. 2007). Our results are relatively consistent with climate suitability projections of 21st-century lodgepole pine and Douglas-fir distributions in Yellowstone, which suggest range reductions and distributional shifts to higher elevations. (Bartlein et al. 1997, Crookston et al. 2010, Coops and Waring 2011, Gray and Hamann 2013, Bell et al. 2014, Hansen and Phillips 2015). While our approach takes a step beyond climate suitability studies by considering the processes that are important during a sensitive life-history stage (regeneration), we still only consider the responses of individual tree species to changing climate and fire. However, the abundance and distribution of a species can be strongly shaped by competitive interactions, particularly at local to landscape scales (Copenhaver-Parry et al. 2017), and process-based models are a promising tool for determining where and why interspecific biotic interactions might modulate how tree species respond to climate change.

What explains changing stand densities?

Postfire stand densities for all three forest types were sensitive to both fire and climate drivers, with fire frequency and size influencing potential establishment and climate conditions largely affecting survival and growth. As hypothesized, warming led to increased density of Douglas-fir in our simulations, particularly when precipitation also increased (Fig. 4). Densification of Douglas-fir regeneration under warmer climate is consistent with expectations for a tree species at the leading edge of its distribution (Hansen and Phillips 2015) and with the fossil pollen record in Yellowstone. Conditions were warmer than present during the early to mid Holocene, and Douglas-fir expanded to higher elevations—but only on andesite substrate (Whitlock 1993). The lack of edaphic constraints on Douglas-fir regeneration in our simulations

suggests other factors (e.g., competition among tree species) may have shaped Douglas-fir distributions in response to past climate variation.

Postfire lodgepole pine stand density was influenced by multiple climate factors, acting in opposing directions. Decreasing annual precipitation, which mainly falls as snow in Yellowstone, increased lodgepole pine densities. Reduced spring snowpack can lead to increased early postfire densities of tree species by lengthening growing seasons (Hansen et al. 2016), when there is sufficient soil moisture and little frost damage. However, soil drying decreased non-serotinous lodgepole pine densities. Effects of soil drying on lodgepole pine seedlings are well documented. Stand densities were substantially reduced in the northern Rockies when recent fires were followed by hot-dry versus cool-wet conditions (Harvey et al. 2016a). Disentangling effects of opposing climate drivers of postfire regeneration could be explored more fully with experimental approaches.

Considered together, our simulations of postfire regeneration suggest that forest-landscape patterns could become increasingly coarse-grained in the future, as climate changes and fires become larger and more frequent. The number and size of non-forest patches could increase, due to regeneration failure, but the surrounding forests may actually become more dense. This could have important consequences for forest susceptibility to subsequent disturbance agents (Seidl et al. 2016a) and the provision of ecosystem services (Turner et al. 2013, Spies et al. 2017). Changes in spatial patterns of forest cover and structure could also be sensitive indicators of forest resilience (Scheffer et al. 2012, Ghazoul et al. 2015, Seidl et al. 2016b). Increased regeneration failure over multiple fire cycles or shifting spatial patterns can indicate slowing of ecosystem recovery and impending transitions to alternate states (Kéfi et al. 2007, Dakos et al. 2011, Ghazoul and Chazdon 2017, Walker et al. 2016). Establishing resilience

indicators for forest systems is particularly important because forests can respond slowly to drivers, and marginal changes may go unrecognized if postfire recovery dynamics are not monitored through time (Hughes et al. 2013, Paine et al. 1998, Lindenmayer et al. 2016).

Conclusions

Tree regeneration is a resilience linchpin in forests where large high-severity disturbances occur (Gauthier et al. 2015, Johnstone et al. 2016, Turetsky et al. 2016). Simulated postfire regeneration of two widespread subalpine conifers was surprisingly resilient to future climate and fire regimes. Multiple drivers were often required for regeneration to fail – distance to seed source, paired with cold temperature for Douglas-fir or with short FRIs for serotinous lodgepole pine (Fig. 2) – and such relationships may well apply to other obligate seeders. It appears that the indirect effects of 21st-century warming, causing an increase in the size and frequency of stand-replacing fire (Westerling et al. 2011, Harvey et al. 2016b), could exceed the direct effects of warming on early postfire conifer regeneration in Yellowstone.

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- 798

799 **Tables**

800 Table 1. Hypotheses of how changing climate and fire regimes will interact to cause postfire
801 regeneration failure in subalpine forest types found throughout western North America (adapted
802 from Johnstone et al. 2016).

Process	Driver	Hypothesized mechanism	Citations
Seed supply	Fire return interval	If fires become more frequent and sequential fires occur before trees mature, then postfire regeneration will be constrained. Serotinous lodgepole pine may be particularly vulnerable due to reliance on an <i>in situ</i> seedbank.	Buma et al. 2013
Seed delivery	Distance to seed source	If patches of stand-replacing fire exceed seed dispersal distances, postfire regeneration may be constrained, especially in the middle of large burned patches. Non-serotinous lodgepole and Douglas-fir may be particularly vulnerable due to their reliance on unburned trees as a seed source.	Harvey et al. 2016a, Turner et al. 1999, 2004, 2016
Seedling establishment	Postfire drought	If drought occurs in the first few years postfire, seedling establishment may be reduced even if seed is abundant. Lower montane sites, which are already warmer and drier, may be especially vulnerable to drought.	Harvey et al. 2016a

805 Table 2. ANOVA results of top models ($AIC_c < 2$) predicting A. frequency of regeneration
 806 failure and B. Density differences between 21st-century and historical periods, if regeneration
 807 was successful. Regeneration failure frequency was logit transformed. Density differences for
 808 serotinous lodgepole pine was transformed to the $\sqrt[9]{}$. Sum of squares, F-values, significance
 809 levels and model adjusted R^2 are presented.

	Douglas-fir			Non-serotinous lodgepole pine	Serotinous Lodgepole pine
	Model 1	Model 2	Model 3	Model 1	Model 1
A. Regeneration failure					
Distance to seed source	3,843.8***	3,877.9***	3,846.9***	2,503.4***	519.0***
	2,634.9	2,634.9	2,634.9	1,868.7	667.7
Climate Period	165.8***	167.3***	165.9***		
	113.7	113.7	113.7		
FRI					68.1***
					131.4
Elevation		1.9		41.4***	16.8***
		1.3		30.9	21.6
Substrate			1.2	16.3***	
			0.4	6.1	
Distance x Climate	58.3***	58.8***	58.3***		
period	79.9	79.9	79.9		
Distance x FRI					61.9***
					238.9
Distance x Elevation				16.3***	
				24.3	
Adj. R^2	0.97	0.97	0.97	0.96	0.88

B. Density differences

	1,225.6***	28.0***	30.8***
Distance to seed source	1.7x10 ⁹	1.1x10 ⁶	94.5
	192.9***	27.1***	
Climate Period	2.7x10 ⁸	5.1x10 ⁵	
			31.1***
FRI			142.9
		24.2***	57.3***
Elevation		9.1x10 ⁵	175.6
	22.4***		
Substrate	3.2x10 ⁷		
	176.8***		
Distance x Climate	2.5x10 ⁸		
period			
			14.4***
Elevation x FRI			132.9
		17.5***	
Distance x Elevation		1.3x10 ⁶	
Adj. R ²	0.95	0.58	0.71

*p<0.05, **p<0.01, ***p<0.001

812 Table 3. Averaged Linear mixed effects regression results of top models ($AIC_c < 2$) predicting
 813 A. frequency of regeneration failure and B. density differences between 21st century and
 814 historical periods, if regeneration was successful. Regeneration failure frequency was logit
 815 transformed. Density differences for serotinous lodgepole pine was transformed to the $\sqrt[3]{}$.
 816 Coefficients of all continuous variables were standardized to z-scores and significance levels are
 817 presented for fixed effects. Standard deviations are presented for random effects

	Douglas-fir	Non-serotinous lodgepole pine	Serotinous lodgepole pine
A. Regeneration failure			
<i>Fixed effects</i>			
Intercept	0.02	-0.003	-0.004
Growing season frost events	0.16***	0.09**	0.14**
Growing season soil water potential		-0.11***	-0.04
Growing season temperature	-0.06**		
Annual precipitation		-0.01	-0.04
Frost events x temperature	0.03		
Frost events x soil water potential			-0.03
Frost events x Precipitation		-0.006	-0.02
<i>Random effects</i>			
FRI			0.37
Distance to seed source	0.95	0.96	0.76
B. Density differences			
<i>Fixed effects</i>			
Intercept	-0.16	0.14	0.06
Growing season frost events		0.14	0.07
Growing season soil water potential		0.30**	-0.01

Growing season temperature	0.47***		
Annual precipitation	0.41***	-0.54***	-0.41***
Precipitation: Temperature	-0.14*		
Frost events: Precipitation		0.22**	0.07
Frost events: soil water potential			0.04
Precipitation: soil water potential			-0.02
<i>Random effects</i>			
FRI		0.26	0.45
Distance to seed source	0.83	0.37	0.38

*p<0.05, **p<0.01, ***p<0.001

Figure legends

Figure 1. Frequency of regeneration failure (%) at postfire-year 30 for Douglas-fir (DF), non-serotinous lodgepole pine (LP-NS) and serotinous lodgepole pine (LP-S) across all simulations. Values are means \pm 2 standard errors.

Figure 2. State space conceptually summarizing conditions that led to postfire-year 30 tree regeneration failure (orange) and success (green) as a function of distance to seed source, fire return interval, and climate period for (A) Douglas-fir, (B) non-serotinous lodgepole pine, (C) serotinous lodgepole pine, three widespread forest types in Rocky Mountain forests.

Figure 3. Frequency of regeneration failure (%) at postfire-year 30 as a function of distance from seed source and fire return interval (FRI) for (A) Douglas-fir, (B) non-serotinous lodgepole pine, (C) serotinous lodgepole pine. Values are means \pm 2 standard errors.

Figure 4. Differences in early postfire (30 year) Douglas-fir stand density between historical and 21st-century climate periods versus 21st century annual precipitation (mm) and growing season mean temperature (°C). Values are predictions from a loess fit.

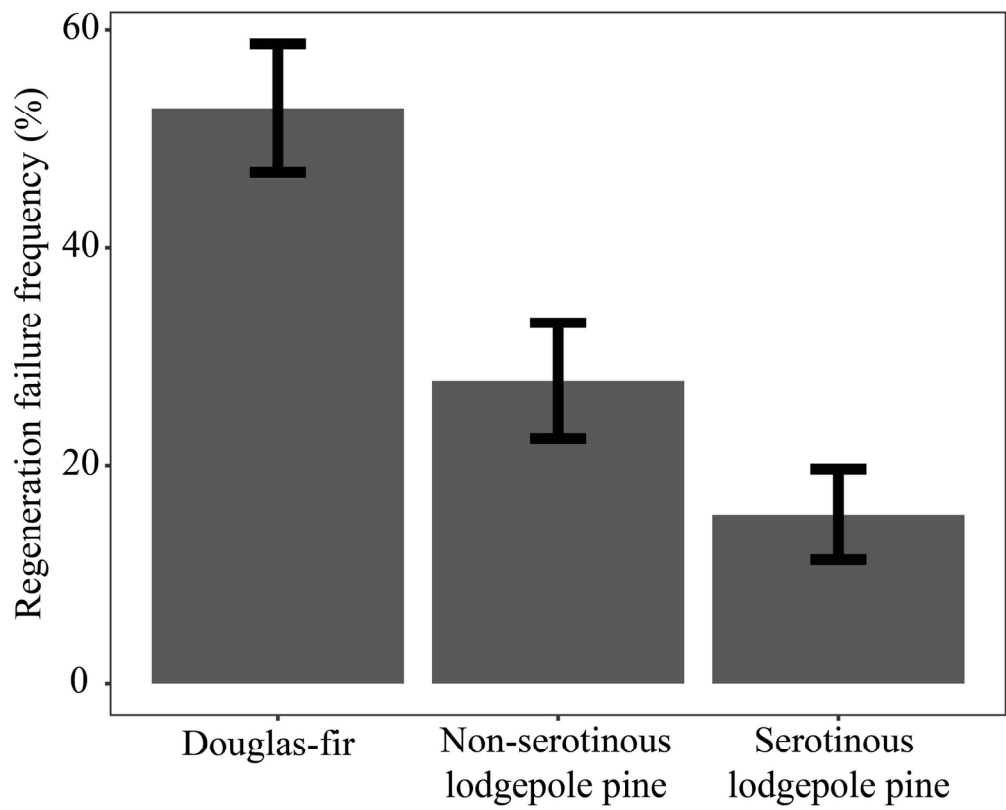


Figure 1. Frequency of regeneration failure (%) at postfire-year 30 for Douglas-fir (DF), non-serotinous lodgepole pine (LP-NS) and serotinous lodgepole pine (LP-S) across all simulations. Values are means \pm 2 standard errors.

87x73mm (600 x 600 DPI)



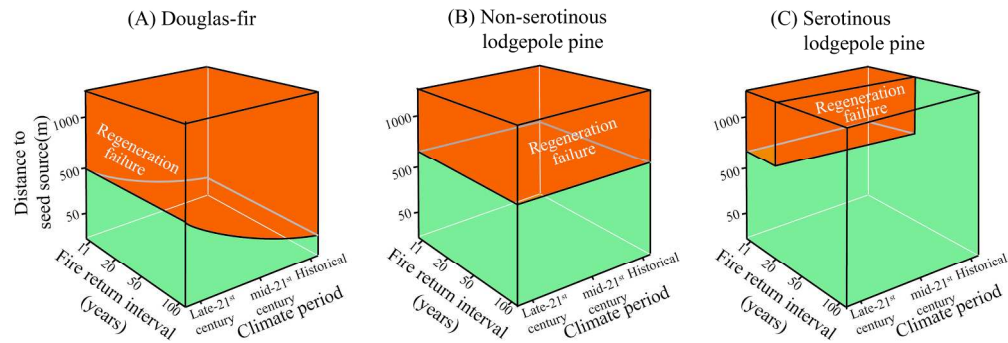


Figure 2. State space conceptually summarizing conditions that led to postfire-year 30 tree regeneration failure (orange) and success (green) as a function of distance to seed source, fire return interval, and climate period for (A) Douglas-fir, (B) non-serotinous lodgepole pine, (C) serotinous lodgepole pine, three widespread forest types in Rocky Mountain forests. Grey scale version available for print.

106x55mm (600 x 600 DPI)

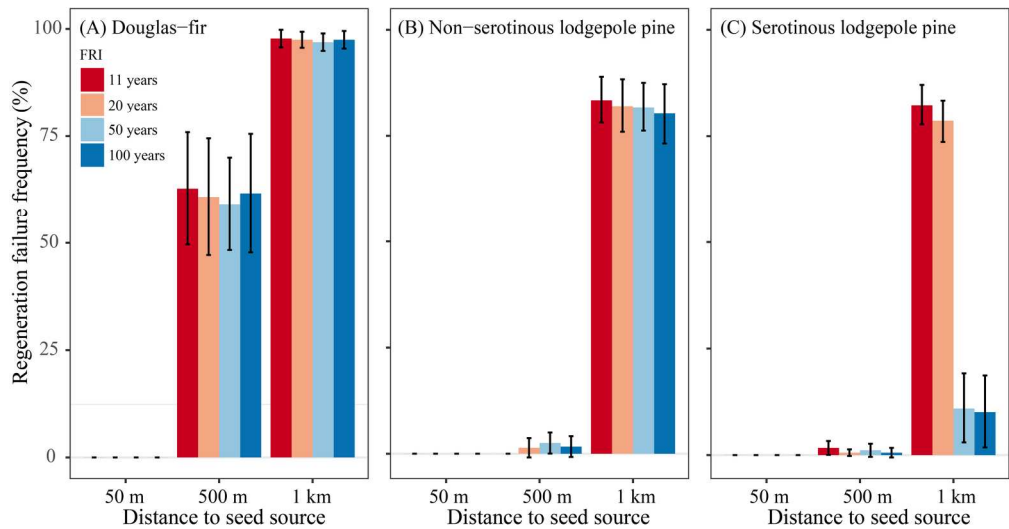


Figure 3. Frequency of regeneration failure (%) at postfire-year 30 as a function of distance from seed source and fire return interval (FRI) for (A) Douglas-fir, (B) non-serotinous lodgepole pine, (C) serotinous lodgepole pine. Values are means \pm 2 standard errors. Grey scale version available for print.

94x49mm (600 x 600 DPI)

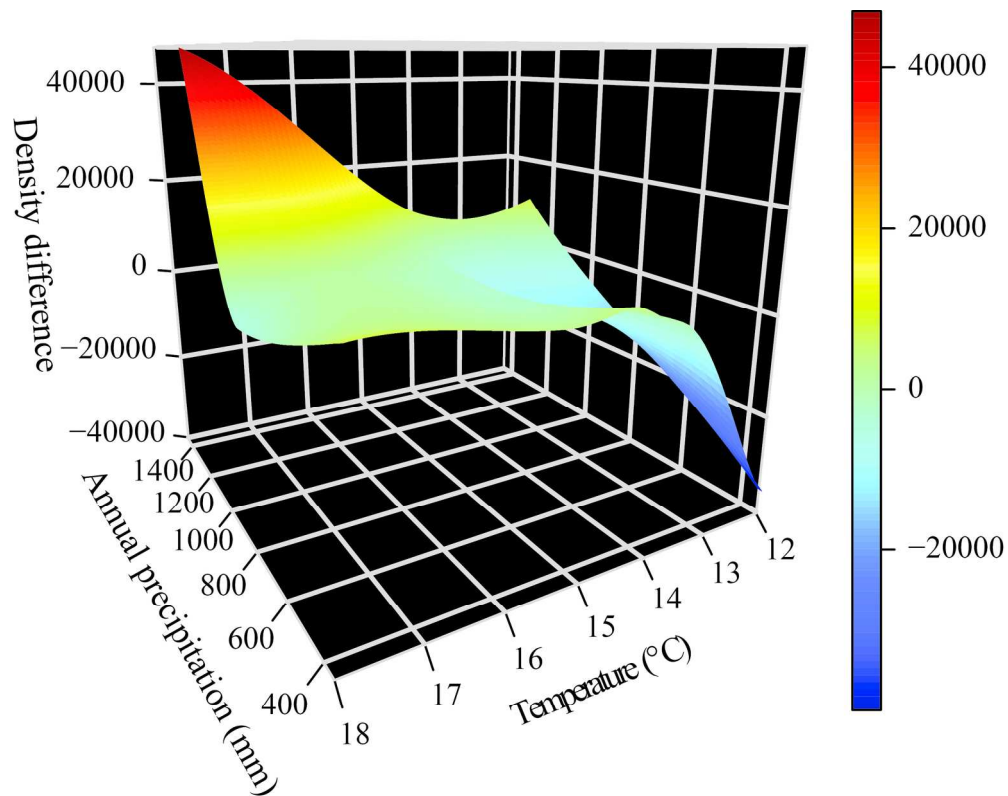


Figure 4. Differences in early postfire (30 year) Douglas-fir stand density between historical and 21st-century climate periods versus 21st century annual precipitation (mm) and growing season mean temperature ($^{\circ}\text{C}$). Values are predictions from a loess fit. Only color available.

89x70mm (600 x 600 DPI)

Appendix S1

Table S1. iLand regeneration module parameters used to explore effects of changing fire regimes and postfire warming/drying on tree regeneration of and Douglas-fir (DF), non-serotinous lodgepole pine (LP-NS), and serotinous lodgepole pine (LP-S) stands in Yellowstone National Park, Wyoming, USA. Extensive model documentation is available at (<http://iland.boku.ac.at/iLand+Hub>) and a full parameter set is available at (https://github.com/whansen3/Hansen_stand_level_archive).

Parameter name	Units	Source	LP-NS	LP-S	DF
<i>Seed production/ dispersal</i>					
Cone bearing age	years	8, 10, 12-13	15	15	55
Seed year interval	years	9, 10, 12; 14-19	1	1	5
Non- seed year fraction	dim[0,1]	9, 10, 12; 14-19	0	0	0.24
Seed mass	mg	10, 11, 12,	4.1	4.1	11.31
Germination rate	dim[0,1]	49, 20-24	0.36	0.36	0.30
Fecundity	sdlings m ⁻²	24-25	115.9	115.9	43.9
Seed kernel a	m	10, 26-30	6	6	30
Seed kernel b	m	10, 26-30	160	160	200
Seed kernel c	dim[0,1]	1	0.05	0.05	0.2
<i>Establishment</i>					
Min temperature	°C	31	-85	-85	-37
Chill requirement	days	31	63	63	56
Min growing degree days	degree days	31	186	186	340
Max growing degree days	degree days	31	3374	3374	3261
Growing degree days base temperature	°C	31	2.9	2.9	3.4
Growing degree days bud burst	degree days	31	116	116	255
Frost free days	days	31	80	80	100
Frost tolerance	dim[0,1]	31	0.9	0.9	0.5
Min soil water potential	MPa	31	-2.3	-2.3	-7
<i>Sapling growth</i>					
Sapling growth a	dim	2,3-7, 32-41	0.05	0.05	0.036
Sapling growth b	m	2,3-7, 32-41	24	24	47
Max number of years under stress	years	This paper	2	2	3
Stress threshold	dim[0,1]	34	0.2	0.2	0.05
Height to diameter ratio	dim	2, 3, 5, 7	72	72	88
Reineke's R	saplings ha ⁻¹	2, 3, 5, 7, 34	14.33	550	500
Reference ratio	dim[0,1]	This paper	0.457	0.457	0.451
<i>Serotiny</i>					
Serotiny formula	dim[0,1]	3	x,20,0,80,1		
Serotiny fecundity		3	30		

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For Review Only

Appendix S2.

We evaluated how well iLand simulated variation in early postfire lodgepole pine and Douglas-fir densities as a function of distance to seed source based on species specific dispersal kernels (Table S1). We compared simulated densities at 50 m, 500 m, and 1 km with early post fire stand densities measured in field surveys throughout Yellowstone (Donato et al. 2016, Harvey et al. 2016a). Stem densities from field surveys declined with distance to seed source and closely matched simulated densities (Fig. S1). Douglas-fir densities declined more quickly than lodgepole-pine densities and no Douglas-fir seedlings established 1 km from seed source in either field surveys or simulations.

Figure S1. Early postfire densities of Douglas-fir and lodgepole pine stands as a function of distance to seed source in (A) field surveys after recent fires in greater Yellowstone (Harvey et al. 2016a, Donato et al. 2016), (B) simulations in iLand.

